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# Effects of forest management on soil carbon: results of some long-term resampling studies

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"**Capsule**": *The effect of forest harvest treatments on regeneration growth and biomass are likely to cause long-term differences in ecosystem carbon.*

## Abstract

The effects of harvest intensity (sawlog, SAW; whole tree, WTH; and complete tree, CTH) on biomass and soil C were studied in four forested sites in the southeastern US (mixed deciduous forests at Oak Ridge, TN and Coweeta, NC; *Pinus taeda* at Clemson, SC; and *P. eliottii* at Bradford, FL). In general, harvesting had no lasting effects on soil C. However, intensive temporal sampling at the NC and SC sites revealed short-tam changes in soil C during the first few years after harvesting, and large, long-term increases in soil C were noted at the TN site in all treatments. Thus, changes in soil C were found even though lasting effects of harvest treatment were not. There were substantial differences in growth and biomass C responses to harvest treatments among sites. At the TN site, there were no differences in biomass at 15 years after harvest. At the SC site, greater biomass was found in the SAW than in the WTH treatment 16 years after harvest, and this effect is attributed to be due to both the N left on site in foliar residues and to the enhancement of soil physical and chemical properties by residues. At the FL site, greater biomass was found in the CTH than in the WTH treatment 15 years after harvest, and this effect is attributed to be due to differences in understory competition. Biomass data were not reported for NC. The effects of harvest treatment on ecosystem C are expected to magnify over time at the SC and FL sites as live biomass increases, whereas the current differences in ecosystem C at the TN site (which are due to the presence of undecomposed residues) are expected to lessen with time. © 2001 Published by Elsevier Science Ltd. All rights reserved.

*Keywords:* Forest; Soil; Carbon; Harvest; Biomass

## 1. Introduction

Forest soil scientists have long been concerned with soil carbon (C) because it is often a master variable determining soil fertility (Pritchett and Fisher, 1987). In recent decades, knowledge of the role of soils as a source or sink for C on a global scale has become vital for assessing changes in atmospheric $CO_2$ concentrations as well (Dixon et al., 1994; Schimel, 1995). Forest soils in North America are of particular interest: Fan ct al. (1998) estimated that North American forests take up 1.7x $10^{15}$g C year$^{-1}$. On an area basis, this figure (3 to 4x Mg C ha$^{-1}$ year$^{-1}$) exceeds the average rates of C accumulation in biomass of US forests (1.4 Mg C ha$^{-1}$ year$^{-1}$; Dixon et al., 1994), suggesting the possibility of soil C accumulation. While there is good information

about the rate of soil C change in specific forested sites (e.g. Richter et al., 1994; Knoepp and Swank, 1997; Trettin et al., 1999), the rate of C accumulation in forest soils on a regional scale is unknown.

In a recent literature review that included a meta analysis, we concluded that forest harvesting, on average, had a slightly positive effect on soil C (Johnson and Curtis, 2001). Significant effects of harvest type and species were noted, with sawlog harvesting causing increases (+18%) in soil C and whole-tree harvesting causing decreases (−6%). In this paper, we review the results of some case studies from a multi-site DOE-funded harvesting study initiated in the late 1970s as part of the fuels from biomass program (Mann et al., 1988). These studies afforded an excellent opportunity to evaluate the long-term effects of harvesting on productivity, soil carbon, and nutrients within a variety of forest ecosystems with excellent control over sampling. The principal investigators, and, in some cases, the field

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technicians who first established these studies oversaw and conducted this resampling, providing excellent control over some of the variables that plague literature reviews such as those described above. Several publications, reports and a PhD thesis have resulted from these and associated studies; the reader is referred to these publications (see References) for details of these specific studies. This paper will summarize the harvesting effects on ecosystem C balances and compare these results to those of the more general reviews described above.

## 2. Materials and methods

The sites included mixed oak forests in Tennessee (TN) and North Carolina (NC); loblolly pine in South Carolina (SC); and slash pine in Florida (FL). Each site was subjected to harvesting in the 1977–1980 period, and vegetation, litter, and soil samples were taken prior to harvest (Mann et al., 1988). The initial treatments varied somewhat between sites. Details of site characteristics, experimental design, and sampling and analysis procedures are given below and summarized in Table 1.

### 2.1. Oak Ridge, TN site

The TN site is located on the Oak Ridge Reservation near Oak Ridge, TN. Mean annual precipitation is approximately 1500 mm, and mean annual temperature is approximately 14.4 °C. The site was a woodland pasture prior to 1942 when it became part of the Oak Ridge

Reservation. Since that time, it has converted to a mixed oak forest (see Table 1 for list of major species). Ages of overstory trees ranged from 50 to 120 years at the time of harvest (Johnson et al., 1982). Soils are deep, highly-weathered Ultisols derived from dolomite (Table 1). The dominant soils, occupying >80% of the area of each watershed, are Fullerton (Typic Paleudults). There are also minor inclusions of Bodine soils (Typic Paleudults) on steeper side slopes and Dewey and Dunmore series (Typic Paleudults) in the lowest slope positions (Johnson et al., 1982). Although these soils are derived from dolomite, they are highly weathered and low in total Ca and Mg (Johnson and Todd, 1987).

In the spring of 1979, prior to harvest, five watersheds ranging in size from 0.25 to 0.54 ha were identified, surveyed, sampled for soils, and inventoried for biomass (Johnson et al., 1982). A total inventory of all trees > 10 cm dbh was conducted on each watershed, and trees < 10 cm were inventoried by establishing four circular 0.0045-ha plots per watershed. Biomass was estimated from the regression equations developed for nearby Walker Branch Watershed (Harris et al., 1973) and rechecked during harvest in 1980 (Johnson et al., 1982). Two 10×10-m plots were established in each watershed and permanently monumented with aluminum stakes for long-term litter and soil sampling. Within each plot, litter and soils were sampled from the centers of three randomly-located 2×2-m subplots, making a total of 12 replicate samples per harvested treatment and six in the reference watershed. Litter was sampled from within a 0.25-m² ring and separated into Oi, Oe, Oa, and wood

Table 1
Locations, vegetation, soils, and treatments at the southeastern sites

| Site | Dominant vegetation | Soils | Treatments[a] |
|------|---------------------|-------|---------------|
| Coweeta, NC | Mixed deciduous *Liriodendron tulipifera* *Quercus velutina* *Q. coccinea* *Q. rubra* dominant | Typic dystrochrepts Typic haplumbrepts | SAW, 1977 WTH, 1980 Resampled 1992 1993, and 1994 |
| Clemson, SC | *Pinus taeda* | Typic kanhapludults | WTH and SAW 1978–1979 Resampled in 1995 |
| Oak Ridge, TN | Mixed deciduous *Q. prinus, Q. alba* *Q. rubra, Q. velutina* *Liriodendron tulipifera* *Acer rubrum, Carya ovata* *C. tomentosa* *Nyssa sylvatica* | Typic paleudults | WTH and SAW 1980 Resampled in 1996 |
| Bradford, FL | *Pinus elliottii* | Ultic alaquods Plinthic paleudults | WTH and CTH, 1981 Resampled in 1996 |

[a] SAW = sawlog harvest; WTH = whole-tree harvest; CTH = complete tree harvest and 10–30 cm. Data analyses were conducted comparing post and pre-treatment levels of soil C and N.

fractions. Soils were then sampled with a bucket auger by depth (0–15, 15–30, and 30–45 cm) at each point. Bulk density and percent gravel were determined on three quantitative pits dug in differing slope positions on the site before treatment.

In the fall of 1980, watersheds 1 through 4 were clearcut. All above-stump material was removed from watersheds 1 and 2, while only sawlogs (>28 cm dib) were removed from watersheds 3 and 4. Watershed 5 was left uncut. Each harvested log, top, and non-commercial tree from watersheds 1 and 2 were weighed at the time of harvest (Johnson et al., 1982). Logging residue was estimated in two ways: (1) as the difference between pre-harvest inventory and weights of biomass removed during harvest, and (2) by sampling five randomly located 2×2-m subplots within the 10×10-m plots previously described. Residue in these plots was weighed by size class (>5, 1–5, and <1 cm), sub-sampled for moisture content, and replaced (Johnson et al., 1982). Regeneration was allowed to proceed naturally from sprouting and seed.

During the spring and summer of 1995 vegetation and soils were resampled. Vegetation was tallied by species and dbh in six randomly-located, nested, circular plots using the Walker Branch protocols (Johnson and Van Hook, 1989). Biomass was estimated using the 1979 allometric equations. Large woody residue remaining on site in 1995 was tallied in two different ways: (1) the 10×10-m plots previously described were relocated, and residue within five of the 2×2-m plots was sampled, excluding those sampled in 1980; and (2) remaining residues were inventoried in 15 2-m diameter circular plots randomly located in the sawlog harvested watershed (Johnson and Todd, 1998b). Each of the 10 10×10-m permanent plots was relocated and litter and soils were sampled by the same two people (Johnson and Todd) using the same protocols as in 1979. A horizon soils were also sampled for bulk density within each 2×2-m subplot using a 2.5-cm diameter coring device. Soils sampled in 1979 and in 1995 were analyzed in 1996 for total C using the Perkin-Elmer 2400 CHN Analyzer.

## 2.2. Bradford, FL site

The research site was located 10 miles west of Starke, FL on JSC Corporation's Bradford Forest. Two experimental watersheds of 3.8 and 4.2 ha size were established in areas comprised by Mascotte (Ultic Alaquod) and Stilson (Arenic Plinthic Paleudult) series soils. In 1981, two harvesting and regeneration regimes were applied to these two watersheds: whole tree harvesting (WTH) and complete-tree harvesting (CTH). In the WTH watershed, all trees including branches and foliage were harvested and the slash remaining on the site was chopped and burned before bedding and planting to slash pine. This treatment simulated a whole

tree harvesting where all of the above-ground biomass was removed. On the CTH watershed, after trees were harvested and before preparing and planting the site, stumps with diameter greater than 15 cm were pulled from the ground and removed from the watershed. This treatment simulated a complete-tree harvest and is estimated to have increased organic carbon removal by 19% and nitrogen removal by 14% over the WTH (Gain, 1987).

To resample this site, sample points were established at 50 m intervals along north-south transect lines located 100 m apart (Shan and Morris, 1998; Shan, 2000). Overstory trees were sampled according to the following protocols. Each sample point served as the center of a 0.0407 ha circular plot. Within this plot, diameters and heights of all trees greater than 5 cm diameter were measured. One tree within each plot was selected for biomass determination and felled. Green weights of stem and branch plus foliage were determined in the field and sub-samples of stem, branch, and foliage collected, sealed in plastic and returned to the laboratory for moisture content determination and nutrient analyses. A total of 17 trees were harvested, which encompassed the diameter distribution of measurement trees. Biomass data from these trees were used to verify the accuracy of a preexisting biomass regression developed on a site adjacent to the study site by Swindel et al. (1979). The equations of Swindel et al. (1979) was used to estimate stem, branch and needle weight for all plots on the basis of measurement data. Nutrient concentrations determined for collected samples were applied to these predictions to estimate tree nutrient content.

In each 0.0407 ha measurement plot, a 2×2 m understory sampling plot was randomly established for understory, litter and soil sampling. Within this plot, all herbs, shrubs, wood vines and trees less than 5 cm diameter were harvested and green weights determined. Sub-samples of stems, branches and leaves were collected, placed in plastic bags and returned to the laboratory for determination of dry weight and nutrient concentration. In each 0.0407 ha measurement plot, a 25×25 cm forest floor sampling plot was located in each of four quadrants. Within each quadrant, the entire forest floor was collected to the surface of the mineral soil. Once the forest floor was removed, mineral soil was collected to 100 cm depth using an 8.0 cm diameter bucket auger. Each soil sample was separated by horizon and analyzed for C using a LECO CNS analyzer (Leco Corporation, St. Joseph, MI).

## 2.3. Clemson, SC site

The SC study was located on the Clemson University Experimental Forest in the upper Piedmont of South Carolina. Treatment areas are in a loblolly pine plantation established on worn-out agricultural fields in 1938. Light thinning from below at ages 22 and 30 years had

increased the original 2×2-m spacing to about 5×5 m. Soil is an eroded phase of the Pacolet fine sandy loam, a thermic typic Kanhapludult. The plantation grew on a site with an aspect of S-SW. Treatments were applied to two small (<2.2 ha each) watersheds about 200 m apart within the larger plantation. Although lower halves of both watersheds were heavily dissected by eroded gullies, sampling was done on the less steep upper portions (average slope of 5–10%), which were less eroded and more uniform in soil and stand characteristics.

In the winter of 1978–1979, both watersheds were harvested, one by WTH, the other by SAW methods. Both watersheds were regenerated naturally by clearcutting with seed-in-place, using prescribed fires to prepare seedbeds prior to harvest. Treatment response was determined by calculating biomass of the regenerating stand at ages 5 and 16 years. Herbaceous biomass at age 5 was estimated by clipping and weighing 40 quadrants (1/4×4 m) randomly located within each treatment. Equations relating ground-line diameter and total height to biomass were developed for loblolly pine and hardwood stems by destructively sampling 20 pine saplings and 20 hardwood sprouts. Equations were applied to ground-line diameter of all stems on five randomly located plots (5×5 m) within each treatment.

Aboveground biomass at age 16 years was estimated using regression equations developed from 16 trees from each treatment. Biomass was estimated from equations applied to diameter-breast-height (1.4 m) measurements of all trees on three randomly located 200 $m^2$ rectangular plots/treatment. Each plot contained 20–30 pine trees. Similarly, dead wood was estimated from regression equations derived from 16 dead trees/treatment.

Soil C content to 1 m depth was estimated in each plot from soil cores (2.5-cm dia) from three points/plot/treatment. Samples were taken at 0–10, 10–30, 30–50, and 50–100 cm depths. Soil mass was adjusted for rock content and root volume determined in previous studies on the area (Parker and Van Lear, 1996). Carbon concentrations were determined on a Perkin-Elmer Model 2400 Elemental Analyzer. Concentrations were multiplied by soil mass to determine C content.

### 2.4. Coweeta, NC site

At the Coweeta site, the SAW site is a 59-ha south facing watershed. Twelve 10-m diameter circular sample plots are located randomly on transects that cross the watershed. Plots represent all of the vegetation types on this large watershed; mixed-oak, cove hardwood and mixed oak-pine. Soil series sampled included the Chandler and Fannin series and the Cullasaja–Tuckasegee complex, which represent Inceptisols and Ultisols. All plots were sampled monthly for 15 months prior to and 18 months following harvest. After which sampling frequency decreased until 1985. All plots were

located and sampled during the dormant season in 1992, 1993, and 1994. Soil samples were collected by depth, 0–10 cm and 10–30 cm.

The whole-tree harvest site is a 0.67 ha area with a southeast aspect. Ten (10×10 m) sample plots were randomly located across the site. Vegetation consisted of mixed-oak and cove hardwood species. Soils on the site are in the Chandler and Tuckasegee series. These soils are classified as coarse-loamy, micaceous, mesic Typic Dystrochrepts and coarse-loamy, mixed, mesic Typic Haplumbrepts, respectively. Sample plots were located on both soil types. Soil samples were collected twice before harvest, in the fall and winter of 1979. The site was logged in March 1980 and soils were sampled every 3 months for 1 year following harvest. Sample collection then became less frequent, ranging from every 6 months to once per year through 1985. All plots were resampled in 1992 and 1994. Soils were collected from two depths, 0–10 cm and 10–30 cm.

Total soil carbon was determined using a LECO CNS2000 CNS analyzer before 1990 and by Perkin-Elmer 2400 CHN Analyzer after 1990. These concentration data were converted to mass using soil type specific bulk density data (Knoepp, unpublished data).

Statistical analyses for SAW and WTH data examined the effect of year on soil C using the GLM procedure in SAS (SAS Institute, 1985). The effect of soil type and the soil type by year interaction were included in the analysis of variance. Differences between pre and post-treatment annual means were determined using Tukey's mean separation test (SAS Institute, 1985). SAW and WTH were also compared with a reference watershed (SREF) in a split plot analysis using the GLM procedure in SAS (SAS Institute, 1985). Only plots within SAW ($n = 7$) and WTH ($n = 7$) on soil types similar to SREF were used in the analysis. All plots represent the mixed oak vegetation type. The plot within watershed error term was used to test for significant differences between watersheds for each year. Differences between WTH and SREF were also examined with analysis of covariance using GLM procedures in SAS (SAS Institute, 1985). Pretreatment WTH data and SREF data collected the same year were used as covariates for each plot.

## 3. Results

### 3.1. Biomass C

Fifteen years after harvest, there was no sign of harvest treatment effect on regeneration biomass at the TN site; indeed, biomass estimates in the SAW and WTH treatment areas were nearly identical (Fig. 1A). The lack of vegetative response to treatments is attributed to the lack of harvesting treatment effect on ecosystem N
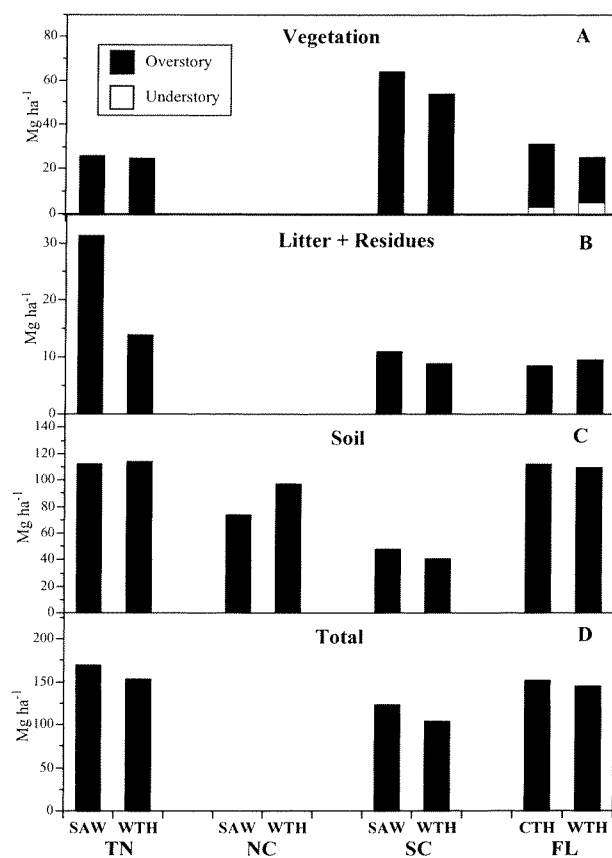
Fig. 1. Ecosystem C contents 15–16 years after harvest.

Table 2
Biomass and nitrogen content of logging debris immediately following sawlog harvest (SAW) and biomass and N content of 16-year-old loblolly pine in sawlog and whole-tree harvest (WTH) at the SC (Clemson, SC) site (after Van Lear, 1998)

| | Biomass (Mg ha$^{-1}$) | N Content (kg ha$^{-1}$) |
|---|---|---|
| Logging residues (SAW) | 20 | 54 |
| *Live biomass at 16 years* | | |
| SAW | 129 | 497 |
| WTH | 107 | 243 |
| Difference | 22 | 254 |

(1 Mg ha$^{-1}$). These biomass differences did not completely offset each other, however; tree biomass dominated and thus total vegetation biomass in the WTH treatment (26 Mg ha$^{-1}$) was 22% less than in the CTH treatment (33 Mg ha$^{-1}$). Reasons for the greater production in the CTH as compared to the WTH treatments at FL are not known; however, understory competition—especially early in stand development—is suspected as the major contributing factor.

Because of the differences in the timing of harvests, no direct comparisons of harvest treatment effects on aboveground biomass were possible at the NC site.

## 3.2. Forest floor and soil C pools

Fifteen years after harvest, there were some differences in forest floor C pools at the TN site due to the presence of logging residues, although 85% of logging residues had decomposed as of that time (Fig. 1B). There were no differences in soil C due to harvest treatment at the TN site, despite the fact that more C was left in logging residues than was originally present in the soils in the SAW treatment (Fig. 1C). The nearly exact accounting of Ca left in logging residues as differences in soil exchangeable Ca$^{2+}$ in the resampling provided good evidence that the lack of difference in soil C was not due to sampling errors (Johnson and Todd, 1998a). Although there were no treatment differences in soil C either before or after harvesting, it appeared that the soils in both the SAW and WTH treatments at TN gained considerable amounts of C over the 15 year period: 9 Mg ha$^{-1}$ in the SAW treatment and 27 Mg ha$^{-1}$ in the WTH treatment (Johnson and Todd, 1998a). Residue C could have accounted for the apparent increases in soil C noted in the SAW treatment, but the even greater increases noted in soil C in the WTH treatment is difficult to explain.

At the NC site, soil C responded to both the SAW and WTH treatments. Total C in the surface 0–10 cm of soil on the SAW treatment site increased an average of 51% compared to pre-treatment levels for 3 years, from 37 to 56 g C ha$^{-1}$ (Fig. 2) (Knoepp and Swank, 1997). Soil C levels remained above pretreatment levels for 18 years, although differences were not significant.

status in these N-limited ecosystems (Johnson and Todd, 1998a).

At the SC site, regeneration biomass was 17% less in the WTH than in the SAW treatments 18 years after harvest (Fig. 1A). The difference in biomass was accompanied by an even greater difference in vegetation nutrient content, especially nitrogen (N), which was 2-fold greater in the SAW compared to the WTH site (Table 2) (Van Lear, 1998). The growth differential between treatments is attributed to greater nutrient uptake on the SAW treatment and enhancement of soil physical and chemical properties by residual logging slash, which occupied 40–60% of the area. Biomass production was high on both treatments because both areas were fully occupied by dense natural pine regeneration soon after harvest. In addition, regeneration utilized decomposing root systems of harvested trees on both treatment areas enhancing their production near old stumps (Van Lear et al., 2000). Decomposing woody debris in tops of harvested trees may have acted in a similar manner.

At the FL site, tree biomass was 27% less in the WTH than in the CTH treatments 15 years after harvest (Shan and Morris, 1998) (Fig. 1A). The reverse was true for understory biomass C that was 100% greater in the WTH treatment (2 Mg ha$^{-1}$) than in the CTH treatment
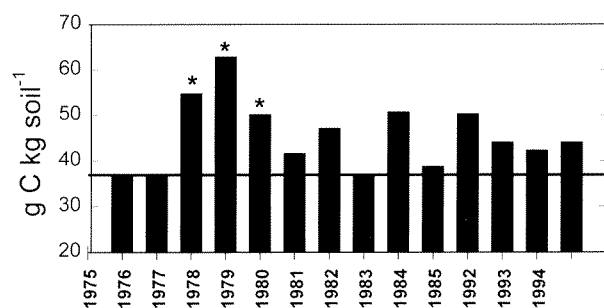
Fig. 2. Changes in soil C in the reference, sawlog (SAW), and whole-tree harvested (WTH) watersheds at Coweeta (from Knoepp and Swank, 1997).

There was a non-significant trend toward decreased soil C on WTH following treatment compared to pre-treatment values (Fig. 2). This decline averaged 13% over the 15-year post-treatment period. To examine the long-term effects of the SAW and WTH treatments, results were compared with a south facing undisturbed reference watershed. Sample plots with similar soil types were used for all comparisons. This analysis showed that the increased soil C observed following the SAW treatment was significant compared to the reference watershed in two of the final three sample collections, 16–18 years following treatment. The long-term response to WTH treatment differed from the short-term response. While the initial response suggested a decrease in soil C following whole-tree harvest, 14 years after treatment soil C in the WTH treatment was significantly greater than in the reference watershed. This was attributed to a decline in soil C content over time in the reference watershed soils.

At the SC site, soil C increased in the first 2 years after harvesting on the SAW treatment, declined in the third year, and then increased to levels above that of the previous plantation (Van Lear et al., 1995). There were no significant differences between treatments in either litter or soil C 16 years after harvest (Fig. 1B). However, large amounts of C in the decomposing root systems of harvested trees were still present on both treatment areas (Van Lear et al., 2000). Large pieces of woody debris from tops of harvested trees could have also contained residual C that would not have been detected by our sampling scheme. As at the TN site, it appears that any inputs of C from aboveground logging slash had been offset by releases of soil C, resulting in no net change in soils C.

At the FL site, there were no differences in litter or soil C (to 1 m depth) or for any individual soil horizon 16 years after harvest (Fig. 1).

### 3.3. Ecosystem C contents

Fig. 1D depicts the ecosystem C contents of the TN, SC, and FL sites 15–16 years after harvest. Because the harvesting treatments did not take place simultaneously at the NC site, biomass C pools are not relevant for this comparison and ecosystems C pools were not calculated. At this stage of stand development, soils comprised a disproportionately large C pool in these sites. In the TN and FL sites, soil C constituted two-thirds to three-quarters of the total ecosystem C capital, and at the SC site, soil C constituted about half of total C capital. Because harvesting treatment had little effect on soil C, it also had little impact on total ecosystem C pools at this stage. At the SC site, ecosystem C in the WTH treatment was 85% of that in the SAW treatment, due mostly to the differences in biomass; and at the FL site, the C content of the WTH site is 95% of that in the CTH site due solely to the differences in biomass. In contrast, ecosystem C in the WTH treatment of the TN site was 90% of that in the SAW treatment due solely due to the presence of a small amount of undecomposed logging residues in the SAW treatment 15 years after harvest.

### 4. Discussion

The extent to which harvesting treatments will cause differences in ecosystem C content at later times will depend largely upon differences in biomass C and how they increase or decrease over time. At the TN site the differences in ecosystem C were due solely to differences in C remaining in logging residues and there is no suggestion that C from these residues will cause any enrichment in soil C. Thus, if the lack of treatment effects on biomass C continue, current differences in ecosystem C due to treatment are expected to decrease. At the SC and FL sites, the differences in ecosystem C content 15–16 years after harvest were due largely to differences in biomass C and thus are likely to increase over time as the relative importance of biomass C increases. Even if the factor(s) causing the differences in growth attenuate with time, the differences in growing stock as of 15–16 years after harvest will likely cause increasing differences in total biomass C and ecosystem C over time.

The results of this study suggest that forest harvesting had little lasting effect on soil C after 15–16 years. The results of the more intensive temporal soil samplings at the NC and SC sites showed that treatment effects on soil C did occur at earlier stages, however and they also showed that soil C varies over time to a considerably greater degree than is commonly assumed. Such interim effects could well have occurred at the TN and FL sites, causing a different interpretation of results than is now the case. Thus, time since harvest is clearly an important factor in assessing harvesting effects on soil C and future studies should always include more frequent sampling than was conducted at the TN and FL sites.

Also, the apparent increases in soil C in both the SAW and WTH treatments at the TN site may have been more easily understood with more frequent sampling.

It appears that longer-term harvesting effects on ecosystem C, where they occur, are manifested primarily as differences in regeneration biomass rather than soil C. Nutrients left in logging residues can contribute to differences in subsequent biomass, as has long been speculated, but other factors such as understory competition and changes in soil physical and chemical properties appear to play a major role. The SC results showed that the N left in residues could not account for the differences in N uptake with treatment, suggesting that (1) growth response was due at least in part to other factors such as improvement in soil physical and chemical properties, and (2) trees in the SAW treatment tapped a source of N in addition to that left in residues. At the TN site, where harvest took place after leaf-fall, N left in woody residues in the SAW treatment (approximately 100 kg ha$^{-1}$) could have provided for the N taken up in the subsequent 15 years (90 kg ha$^{-1}$); however, there were no differences in tissue N concentration, vegetation N content, or biomass between the SAW and WTH treatments after 15 years. Thus it appears that N left in woody residues at the TN site had no benefit to the regenerating forest. The differences in biomass in the harvesting treatments at FL were clearly not related to nutrients left in residues and were probably the result of differences in understory vegetation and competition with planted pine seedlings. Research conducted on similar flatwoods sites has found significant differences in tree growth when understory vegetation is controlled. Thus, while nutrient status is certainly an important growth factor in all these ecosystems, nutrients are not the sole drivers of biomass response to harvest treatments.

## 5. Conclusions

The results of this intensive series of studies suggest that:

1. Nutrients are not the sole drivers of regeneration response to harvesting method; other factors such as effects on soil properties and understory competition play a major role as well.
2. The differences in regeneration biomass due to harvest treatment are likely to cause long-term large differences in ecosystem C at later stages of stand development, even if the initial causes of the differences lessen with time.
3. Differences in litter C due to logging residues lessen with time and apparently do not contribute much to large or long-lasting differences in soil C.

4. The long-term effects of forest residues on ecosystem C pools, when they occur, will be manifested primarily as differences in biomass rather than soil or litter C.

## Acknowledgements

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